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Spatiotemporal variations of tenebrionid beetles (Coleoptera: Tenebrionidae) in the Gobi desert, Northwest China

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Abstract: Tenebrionid beetles represent a crucial arthropod taxon in the Gobi desert ecosystems owing to their species richness and high biomass, both of which are essential for maintaining ecosystem health and stability. However, the spatiotemporal variations of tenebrionid beetle assemblages in the Gobi desert remain poorly understood. In this study, the monthly dynamics of tenebrionid beetles in the central part of the Hexi Corridor, Northwest China, a representative area of the Gobi desert ecosystems, were monitored using pitfall trapping during 2015–2020. The following results were showed: (1) monthly activity of tenebrionid beetles was observed from March to October, with monthly activity peaking in spring and summer, and monthly activity periods and peak of tenebrionid beetle species exhibited interspecific differences that varied from year to year; (2) spatial distribution of tenebrionid beetle community was influenced by structural factors. Specifically, at a spatial scale of 24.00 m, tenebrionid beetle community was strongly and positively correlated with the dominant species, with distinct spatial distribution patterns observed for *Blaps gobiensis* and *Microdera kraatzi alashanica*; (3) abundance of tenebrionid beetles was positively correlated with monthly mean precipitation and monthly mean temperature, whereas monthly abundance of *B. gobiensis* and *M. kraatzi alashanica* was positively correlated with monthly mean precipitation; and (4) the cover of *Reaumuria soongarica* (Pall.) Maxim. and *Nitraria sphaerocarpa* Maxim. had a positive influence on the number of tenebrionid beetles captured. In conclusion, monthly variation in precipitation significantly influences the community dynamic of tenebrionid beetles, with precipitation and shrub cover jointly determining the spatial distribution pattern of these beetles in the Gobi desert ecosystems.

Keywords: Gobi desert; precipitation change; tenebrionid beetles; temporal dynamics; spatial pattern

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1 Introduction

Beetles are among the most diverse animal groups in desert ecosystems, with tenebrionid beetles being a prominent ground beetle group characterized by a wide distribution range, high species

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richness, complex morphological differentiation, and diverse life forms (Twardowski et al., 2017). Tenebrionid beetles are primarily found in desert and semi-desert areas, where they function as key consumers and primary decomposers. Along with ants, tenebrionid beetles are omnivorous arthropods, whose abundance and biomass are the highest among desert arthropods, playing a pivotal role in desert ecosystem food webs (Polis, 1991; Whitford, 1993; Feng et al., 2022; Ren et al., 2024a). Additionally, tenebrionid beetles are vital for the survival and reproduction of vertebrates, such as reptiles, birds, and mammals, as they provide essential food and water resources in desert ecosystems (Groner and Ayal, 2001; Valdez, 2020).

The assemblage of tenebrionid beetles across various spatial scales is influenced by changes in shrub species, shrub coverage, and soil texture. Furthermore, variations in precipitation affect soil moisture and temperature, which in turn influence the response of tenebrionid beetles to vegetation and soil conditions (Liu et al., 2012, 2015; Ren et al., 2024b). Tenebrionid beetles represent the most important arthropod groups in the Gobi desert of Northwest China, and their activities and populations depend on the season and shrub presence and species (Liu et al., 2010). Arid and hyper-arid shrubs, which are the dominant plant species in the Gobi desert, are typically distributed in strips or patches with less than 10.00% vegetation cover. Notably, the impacts and regulatory roles of interactions among precipitation, shrubs, and soil conditions with respect to tenebrionid beetle assemblages at different spatial and temporal scales remain poorly understood. Therefore, long-term data on the mutual feedback relationship between tenebrionid beetle assemblages and climate, vegetation, and soil factors in the Gobi desert are crucial for understanding the roles of these beetles in maintaining the stability and biodiversity of desert ecosystems. Habitat heterogeneity provides diverse ecological niches that facilitate the coexistence of multiple arthropod species in desert ecosystems. Additionally, pattern-process analyses can help to reveal the mechanisms underpinning biodiversity maintenance (Decaëns, 2010; Gao et al., 2018). In recent years, various researchers have investigated the population dynamics of arthropods, such as ground beetles and soil dwelling beetles, and corresponding influencing factors in forest land, grassland, and farmland ecosystems. However, knowledge regarding the population changes of ground beetles in desert ecosystems remains limited (Zhu et al., 2017; Hu et al., 2018).

Deserts, representing one of the most heterogeneous habitats, experience variations in resources due to precipitation fluctuations and interactions with shrubs and animal nests. These variations considerably affect the population dynamics of desert arthropods, especially tenebrionid beetles. Shrubs provide food resources, along with shelter from predators and thermal stress, thereby positively influencing the activity of tenebrionid beetles in arid and semi-arid areas. Annual and seasonal variations in precipitation and temperature can alter the extent of tenebrionid beetles' dependence on shrubs (Mazía et al., 2006; Bartholomew and El Moghrabi, 2018). At a regional scale, desert vegetation cover, community structure, and soil texture are the main factors influencing the aggregation and changes in tenebrionid beetle assemblages (Stapp, 1997). Variations in the intensity of bird predation and the destruction of landscape may also influence the sensitivity of tenebrionid beetles with different body sizes to the changes in vegetation cover (Groner and Ayal, 2001; Sackmann and Flores, 2009; Shelef and Groner, 2011; Lescano et al., 2017). Significant regional and interspecific variations exist in the responses of desert arthropods, such as tenebrionid beetles and ants, to the changes in precipitation. Moreover, omnivorous arthropods like beetles and ants may exhibit a delayed response to annual precipitation fluctuation (Barrows, 2012; Kwok et al., 2016; Gibb et al., 2019; Lin et al., 2022). The bottom-up effect (via the carrying capacity) of desert precipitation increases resource availability, which, in combination with resource enhancement by shrubs and improved habitat conditions, influences the assemblage of tenebrionid beetles. Concurrently, the top-down effect (via biological rate) of predators, such as birds and mammals, is intensified, facilitating the coexistence of multiple desert animal species (Gibb et al., 2022). Considering these aspects, this study focuses on typical desert tenebrionid beetles in the central part of the Hexi Corridor, China. The monthly dynamic changes and main factors affecting tenebrionid beetle assemblages in the Gobi desert were evaluated.

Our goal is to provide scientific basis and data support for biodiversity conservation in desert ecosystems. Therefore, the aims of the study are: (1) to explore the seasonal variations in desert tenebrionid beetle community, which affects the spatial aggregation patterns of these beetles; (2) to examine the influence of climate and shrub coverage on the aggregation of desert tenebrionid beetles; and (3) to study the interactions among precipitation, temperature, and shrubs, and their influence on the aggregation patterns of desert tenebrionid beetles.

2 Materials and methods

2.1 Study area

The study was conducted in the National Sandy Land Closure Protection Area, located in the northern arid desert of Linze County, Gansu Province, Northwest China (39°24′52′′N, 100°07′04′′E). The reserve was established in 2005 with the objective of preventing desertification and protecting the rare flora and fauna resources endemic to the desert. The study area lies 1350 m a.s.l. and experiences a temperate continental arid desert climate. Annual precipitation varies significantly, with sparse snowfall in winter and rainfall predominantly concentrated in summer and autumn. Mean annual precipitation was 117.0 mm, with 79.70% of the total rainfall occurring between June and September during 2011–2020 (Fig. 1). In 2016 and 2018, mean annual precipitation amounts were 65.4 and 81.0 mm, respectively. In contrast, mean annual precipitation in 2019 was 130.8 mm. Annual mean temperature is 7.6°C, with values from 2011 to 2020 being 8.1°C–9.5°C. Annual mean temperature during 2015–2017 was significantly higher than the overall annual mean temperature. Annual evaporation is 2390.0 mm, approximately 20.4 times the annual precipitation (Lin et al., 2022; Chen et al, 2024). Groundwater depth ranges from 10 to 12 m. Soil type is grey-brown desert soil, with coarse sand, fine sand, and silt and clay contents of 38.40%, 55.30%, and 6.30%, respectively.

Vegetation in the study area consists mostly of arid and hyper-arid shrubs, such as *Reaumuria soongarica* (Pall.) Maxim. and *Nitraria sphaerocarpa* Maxim., with a distinct patchy or striped distribution pattern. The most important vertebrate taxa in the Gobi desert include *Phrynocephalus przewalskii*, *Pica pica*, *Oenanthe isabellina*, *Oenanthe desert*, *Lanius sphenocercus*, *Podoces hendersoni*, *Hemiechinus auratus*, and *Vulpes corsac*. In terms of the abundance, biomass, and species richness, tenebrionid beetles are among the dominant arthropod taxa in the Gobi desert (Liu et al., 2010) and have been noted to play a crucial role as consumers and food resources for desert reptiles, birds, and mammals (Lin et al., 2022; Ren et al., 2024b).

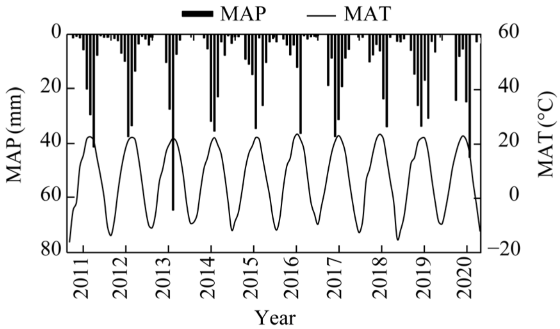

Fig. 1 Monthly mean precipitation (MAP) and monthly mean temperature (MAT) changes in the Gobi desert from January to December during 2011–2020

2.2 Tenebrionid beetle collection and monitoring of environmental elements

In 2012, a long-term monitoring site was established in the study area, to monitor the distribution and diversity of ground arthropods in the Gobi desert (Ren et al., 2024a). First, a 60 m×120 m area was selected for ground arthropod sampling. Subsequently, 72 sampling plots with an area of

8 m×8 m was established in the study area, and a pitfall trap was placed at the centre of each plot. From January 2015 to December 2020, tenebrionid beetles were collected monthly for 7 consecutive days per sampling period using the pitfall trap. The trap preservative was replenished every 3 d using a 75.00% alcohol solution (Liu et al., 2010). The collected beetles were preserved in polyethylene terephthalate vials containing 75.00% alcohol solution and identified to the species level in the laboratory using relevant taxonomic references (Zheng and Gui, 1999; Ren and Ba, 2010; Ren, 2016). The body length of each beetle was measured using a vernier calliper. Meteorological data, including annual and monthly mean temperature and precipitation during 2015–2020, were obtained from the Linze Inland River Basin Research Station, part of the Chinese Ecosystem Research Network. Vegetation composition and coverage for each of the 72 sampling plots in the study area were determined. Due to the annual and seasonal variations of precipitation, herbaceous layer is predominantly composed of annual species, which results in considerable variation in herbaceous diversity and cover. In this study, we focused on shrub species, cover, and density. For each 8 m×8 m plot, we measured the length, width, and height of the crown. Five soil samples in the 0–10 cm depth were extracted near the trap in each plot using a soil auger, combined into a single soil sample, and returned to the laboratory for air drying to determine the soil texture and soil mechanical composition.

2.3 Data analysis

The numbers of tenebrionid beetles captured in the 72 traps from January 2015 to December 2020 were recorded. We classified tenebrionid beetle species as dominant (>10.00%), common (1.00%–10.00%), or rare (<1.00%) based on their proportion to the total number of individuals in the community. Annual and monthly catches, as well as the species richness of tenebrionid beetles, were determined per trap, and the number of catches for each tenebrionid beetle species was also determined per trap. Differences in community composition and contribution of dominant species to the tenebrionid beetle community during 2015–2020 were analyzed using permutational multivariate analysis of variance (PERMANOVA) and similarity percentage (SIMPER) multivariate statistical analyses. Statistical analyses were performed using the paleontological statistics (PAST) v.4.13 software package. Correlations of annual and monthly abundance of tenebrionid beetles with annual and monthly precipitation and temperature were determined through correlation and regression analyses, performed using the SPSS v.21.0 software.

Changes in the assemblage of tenebrionid beetles captured during 2015–2020 were analyzed using a semi-variance function and Moran's *I* value. The semi-variance function indicates the degree of spatial variation within tenebrionid beetle community. Main coefficients of variogram model include nugget, sill, range, and spatial heterogeneity (SH). Nugget in a semi-variance function represents the measurement error or spatial variation when the interval distance is smaller than the sampling interval. Sill is the maximum semi-variance of variogram model, indicating the spatial autocorrelation structure. Range is the distance at which variogram model reaches the sill, indicating the spatial autocorrelation distance. SH reflects the proportion of variation in spatial autocorrelation, with values of <25.00%, 25.00%–75.00%, and >75.00% indicating weak, moderate, and strong spatial autocorrelation, respectively (Gao et al., 2018; Hu et al, 2018; Ren et al, 2024a). Results of analyses have indicated that at SH<25.00%, spatial variance attributable to stochastic factors (such as dispersal and disturbance) is considerably higher than that associated with structural factors (such as topography, climate, and soil). In contrast, at SH >75.00%, spatial variance associated with structural factors is considerably higher than that caused by stochastic factors. SH values between 25.00% and 75.00% indicate that spatial variance is attributable to both structural and stochastic factors (Wang et al., 2016). Ordinary Kriging interpolation was used to map the spatial distribution patterns of tenebrionid beetle community across different years, comparing patch shapes, sizes, and spatial patterns. We performed calculations based on semi-variance function, semi-variance function map, and spatial Kriging interpolation map using geostatistics (GS+) v.9.0 software. Spatial autocorrelation analysis was performed using Moran's *I* value to quantitatively describe the spatial dependence of beetle

communities and identify any spatial clustering within sample plots. In general, Moran's *I* values range from –1 to 1, where 0 represents a uniform distribution within the community with no spatial autocorrelation. Values greater or smaller than 0 indicate positive or negative spatial autocorrelation within the community, representing a clustered or discrete spatial pattern. A higher absolute value corresponds to a greater degree of spatial autocorrelation (Sun et al., 2022). In this work, Moran's *I* value was computed and plotted using the spdep, vegan, ade4, and sp packages in R v.4.2.2 software.

3 Results

3.1 Tenebrionid beetle assemblage

A total of 11,941 tenebrionid beetles, representing 8 species, were captured in 72 traps between January 2015 and December 2020 (Table 1). The dominant species were *Blaps gobiensis* and *Microdera kraatzi alashanica*, accounting for 38.24% and 39.72% of the total tenebrionid beetles captured, respectively. The common species included *Anatolica sternalis*, *Cyphogenia chinensis*, *Pterocoma loczyi*, and *Sternotrigon kraatzi*, representing 9.28%, 1.62%, 7.33%, and 3.12% of the total tenebrionid beetles, respectively. Rare species, namely *Anatolica potanini* and *Platyope victori*, constituted only 0.69% and 0.02% of the total individuals. *B. gobiensis* and *M. kraatzi alashanica* were the main large and small beetle species in the Gobi desert, constituting 65.30% and 88.20% of the total catches during 2015–2020, respectively. These two specifies exhibited high abundance during 2017–2019 but lower abundance in 2016 and 2020 (Table S1).

Table 1 Number of individuals and species composition of tenebrionid beetles captured during 2015–2020 in the Gobi desert, Northwest China

Tenebrionid beetles	Number of individuals	Relative abundance (%)	Feeding type	Body size	Period of activity
Anatolica potanini	82	0.69	Omnivore	Middle	Day
Anatolica sternalis	1108	9.28	Omnivore	Middle	Day
Blaps gobiensis	4566	38.24	Omnivore	Large	Night
Cyphogenia chinensis	193	1.62	Omnivore	Large	Night
Microdera kraatzi alashanica	4743	39.72	Omnivore	Small	Night
Platyope victori	2	0.02	Omnivore	Middle	Day
Pterocoma loczyi	875	7.33	Omnivore	Middle	Day
Sternotrigon kraatzi	372	3.12	Omnivore	Large	Night

3.2 Dynamic changes in tenebrionid beetle community

Activity periods of tenebrionid beetles during 2015–2020 spanned from March to October. Significant annual variations and interspecific differences in the activity periods of tenebrionid beetle species were observed (F=35.04, P<0.001), which were related to their biological characteristics. All 8 beetle species were omnivorous. However, variations in their daily, monthly, and annual activity rhythms were observed (F=12.28, P<0.001). Large and small beetle species, including *B. gobiensis*, *C. chinensis*, *S. kraatzi*, and *M. kraatzi alashanica* were observed to be active at night, dawn, or dusk. In contrast, medium-sized beetle species, including *A. sternalis*, *A. potanini*, *P. victori*, and *P. loczyi*, were observed to be active during the day. These tenebrionid beetle species use shrubs and rodent burrows to escape temperature stress and avoid predators. At the annual scale, activity periods of *B. gobiensis* were from April to October, whereas *A. sternalis* and *M. kraatzi alashanica* were active from March to September (Fig. 2).

Activity periods of *P. loczyi* were from April to July, with minimal annual variation (Fig. 2). Monthly captures of *B. gobiensis* during 2015–2020 showed bimodal or multimodal patterns, with peaks observed between April and August (Fig. 2). Monthly capture counts of medium-sized beetles *A. sternalis* and *P. loczyi* showed a single peak (Fig. 2). Peak monthly catches of *A.*

sternalis and *P. loczyi* occurred in April–May and May, respectively (Fig. 2). Monthly captures of small beetle (*M. kraatzi alashanica*) also exhibited single, double, or multiple peaks, with peak periods between April and August (Fig. 2). *B. gobiensis* and *M. kraatzi alashanica* exhibited lifecycles of 1–2 and 1–3 generations per year, respectively.

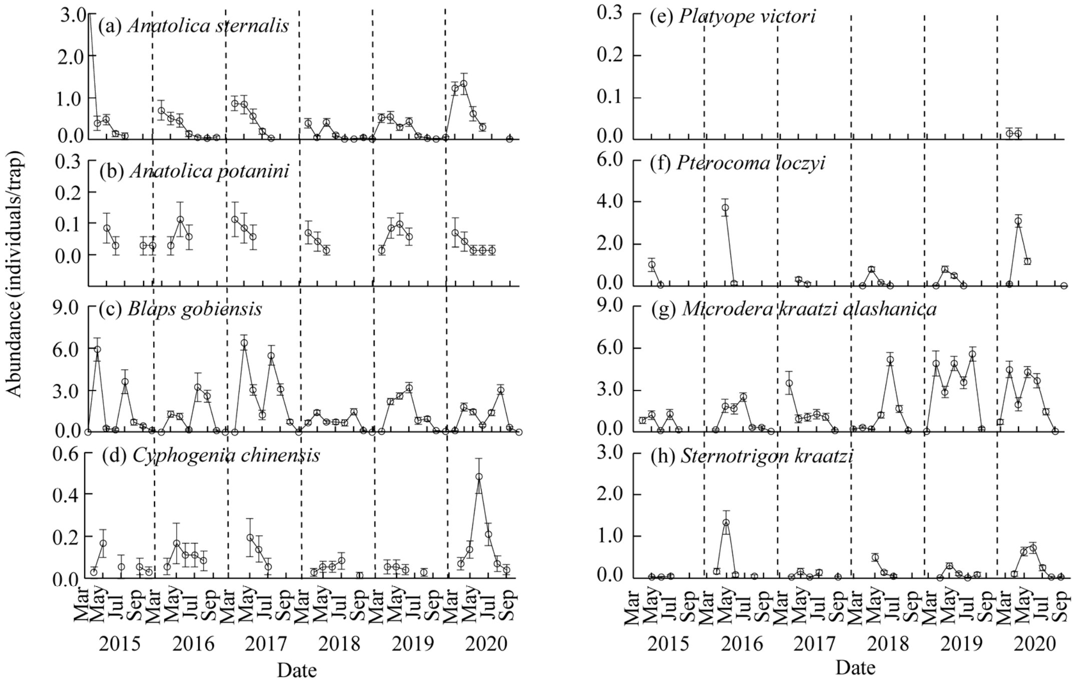

Fig. 2 Abundance of 8 tenebrionid beetle species captured from March 2015 to October 2020 in the Gobi desert, Northwest China. (a), *Anatolica sternalis*; (b), *Anatolica potanini*; (c), *Blaps gobiensis*; (d), *Cyphogenia chinensis*; (e), *Platyope victori*; (f), *Pterocoma loczyi*; (g), *Microdera kraatzi alashanica*; (h), *Sternotrigon kraatzi*. Bars are standard errors.

Community composition of tenebrionid beetles changed significantly during 2015–2020 (F=28.53, P<0.001). Additionally, notable differences in the community composition of tenebrionid beetles were observed between years (P<0.050). According to SIMPER analysis, the average dissimilarity of tenebrionid beetle community ranged from 38.30% to 63.10% during 2015–2020. Furthermore, *B. gobiensis*, *M. kraatzi alashanica*, *A. sternalis*, and *P. loczyi* were the main species contributing to the differences in tenebrionid beetle communities between years. These four tenebrionid beetle species, particularly *B. gobiensis* and *M. kraatzi alashanica*, accounted for 57.50%–83.50% of the observed differences in community composition between years. The abundance of tenebrionid beetles was significantly higher in 2017, 2019, and 2020 than in 2015, 2016, and 2018 (F=35.65, P<0.001). Variations in the species richness and diversity index of tenebrionid beetles were similar to those in the abundance of tenebrionid beetles, with significant increases in 2016, 2018, 2019, and 2020 compared with 2015 and 2017 (Fig. S1). Significant differences were observed in the abundance of 8 tenebrionid beetle species, except for *A. potanini* and *P. victori*. The abundance of *C. chinensis*, *P. loczyi*, and *S. kraatzi* followed a similar trend. These 3 beetle species were significantly more abundant in 2020 than in previous years (Fig. S2).

3.3 Spatial patterns of tenebrionid beetles

Nugget values in semivariogram analysis of dominant tenebrionid beetles species during 2015–2020 were small, indicating that the spatial scale and plot settings were appropriate (Table 2). Spatial distribution of tenebrionid beetles was predominantly influenced by structural factors (Table 2). Variation range of optimal model for semivariogram analysis was between 9.54 and

21.27 m. Semivariogram models for the number of tenebrionid beetles captured in 2018 and 2019 exhibited the narrowest and broadest variation ranges, respectively (Table 2). In years with reduced precipitation, the range of tenebrionid beetles increased, while increased precipitation resulted in a narrower and more stable range. In 2016, SH value of *B. gobiensis* captured was 71.50%. In 2015 and during 2017–2020, SH values of *B. gobiensis* ranged from 87.60% to 100.00%. Spatial distribution of *B. gobiensis* was predominantly influenced by structural factors (Table 2), with optimal semivariogram model ranging from 12.18 to 22.26 m and the lowest range observed in 2016 (Table 2). SH values of *M. kraatzi alashanica* ranged from 88.20% to 100.00%. In other words, spatial distribution of *M. kraatzi alashanica* was predominantly influenced by structural factors (Table 2). Range of optimal semivariogram model was between 8.76 and 25.50 m, with the lowest and highest ranges observed in 2019 and 2018, respectively (Table 2). Except for *B. gobiensis* in 2016 and *A. sternalis* in 2017, for which SH values ranged from 25.00% to 75.00%, SH values of *C. chinensis* were generally above 75.00% across different years, indicating that structural factors controlled its spatial distribution (Table 2). In 2019, a significant negative correlation was observed between *B. gobiensis* and *M. kraatzi alashanica*, indicating opposing spatial aggregation patterns. Decreased annual precipitation led to a more dispersed spatial distribution of these species, while increased precipitation resulted in a more concentrated distribution, with their aggregation areas being opposite. Ordinary Kriging interpolation map showed that in 2015 and 2018, the spatial distribution of tenebrionid beetles was not significantly clustered, whereas a clustered distribution was observed in 2016, 2017, 2019, and 2020 (Fig. 3). Tenebrionid beetles exhibited positive spatial autocorrelation at a scale of 24.00 m, with almost no spatial autocorrelation observed between 40.00 and 96.00 m (Fig. 4). Variation in spatial patterns in 2016, 2017, 2019, and 2020 was similar, i.e., spatial correlation initially decreased and then increased with increasing sample distances.

Table 2 Results of semi-variance analysis on the community abundance and dominant species of tenebrionid beetles during 2015–2020 in the Gobi desert, Northwest China

Group	Model	Nugget	Sill	Range (m)	SH (%)
Tenebrionid beetle community					
2015	Gau	0.08	2.15	11.78	96.20
2016	Exp	0.04	0.42	19.08	89.30
2017	Exp	0.02	0.34	16.41	92.40
2018	Exp	0.00	0.16	21.27	99.10
2019	Sph	0.01	0.11	9.54	96.50
2020	Gau	0.01	0.16	11.76	91.30
Tenebrionid beetle species					
Blaps gobiensis					
2015	Sph	0.10	2.59	12.18	96.30
2016	Exp	0.75	2.63	22.26	71.50
2017	Sph	0.00	1.54	12.75	100.00
2018	Sph	0.10	0.79	12.68	87.60
2019	Sph	0.08	1.15	14.41	93.10
2020	Exp	0.09	0.70	13.98	87.80
Microdera kraatzi alashanica					
2015	Sph	0.00	1.51	9.54	100.00
2016	Sph	0.00	1.50	9.54	100.00
2017	Exp	0.12	2.69	13.14	95.50
2018	Exp	0.10	0.82	25.50	88.20
2019	Exp	0.19	1.59	8.76	88.20
2020	Exp	0.10	1.11	12.48	90.70

Note: Gau, Exp, and Sph, are the Gauss, exponential, and spherical models, respectively; SH is spatial heterogeneity.

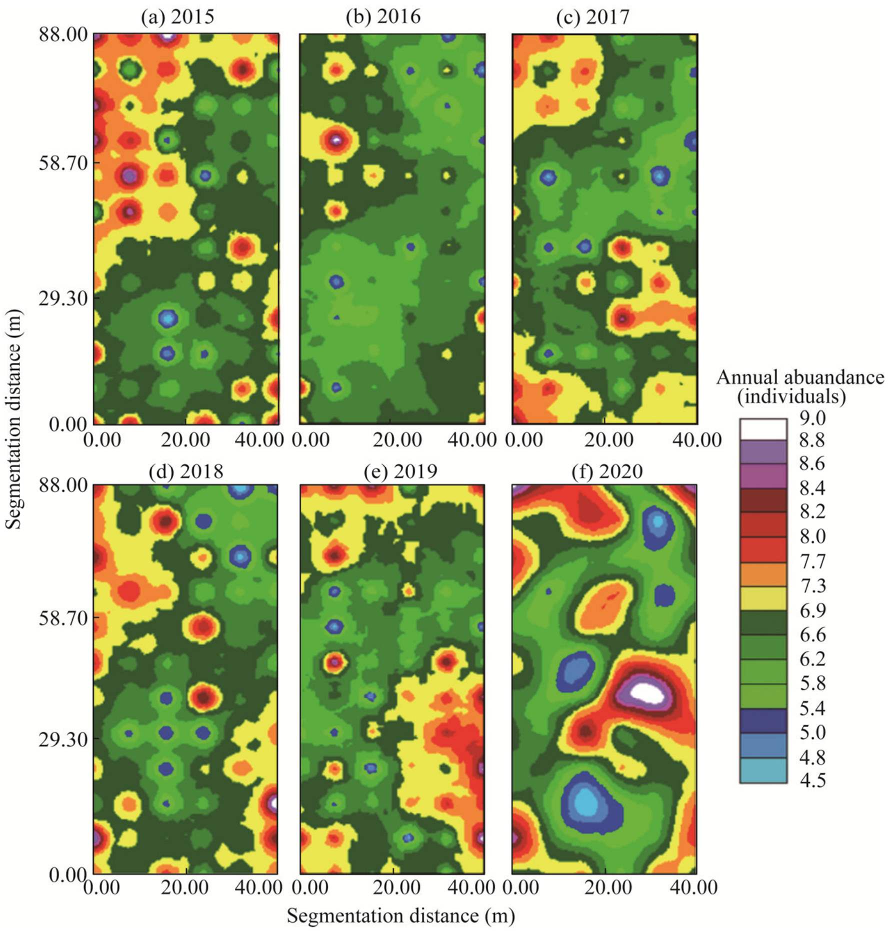

Fig. 3 Kriging map of annual abundance of tenebrionid beetles during 2015–2020 in the Gobi desert, Northwest China. (a), 2015; (b), 2016; (c), 2017; (d), 2018; (e), 2019; (f), 2020.

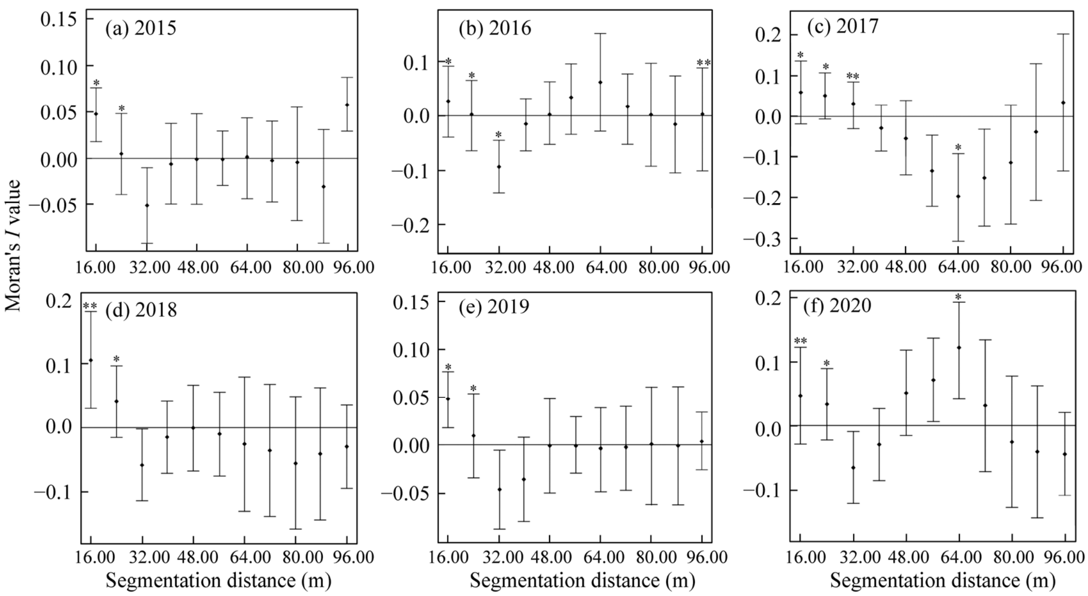

Fig. 4 Moran's *I* value of annual abundance of tenebrionid beetles during 2015–2020 in the Gobi desert, Northwest China. (a), 2015; (b), 2016; (c), 2017; (d), 2018; (e), 2019; (f), 2020. *, $P<0.05$ level; **, $P<0.01$ level. Bars are standard errors.

3.4 Factors influencing spatial and temporal distributions of tenebrionid beetles

Correlations between tenebrionid beetle community and dominant species, as well as annual mean temperature and annual mean precipitation, were weak (Table 3). Additionally, both abundance and species richness of tenebrionid beetles were strongly and positively correlated with monthly mean precipitation and mean temperature (Table 3). Similarly, abundance of *B. gobiensis* was strongly and positively correlated with both monthly mean precipitation and mean temperature, abundance of *M. kraatzi alashanica* was strongly and positively correlated with monthly mean temperature (Table 3). Two dominant shrub species in the Gobi desert are *R. soongarica* and *N. sphaerocarpa*. Our results indicated that the presence of these shrubs influenced the inter-annual variation in the activity of tenebrionid beetles. A significant positive correlation between species richness of tenebrionid beetles and *R. soongarica* cover was observed in 2016, while both abundance and species richness of tenebrionid beetles were significantly and positively correlated with *R. soongarica* cover in 2018 (Table 4). In other years, correlations of abundance and species richness of tenebrionid beetles with *R. soongarica* cover were relatively weak. In 2019, abundance of *M. kraatzi alashanica* showed a significant positive correlation with *R. soongarica* cover, whereas abundance of *B. gobiensis* was weakly correlated with *R. soongarica* cover. Distribution of tenebrionid beetles was positively correlated with *N. sphaerocarpa* cover in 2016, 2017, and 2018 (Table 4). Furthermore, both abundance and species richness of tenebrionid beetles were significantly and positively correlated with *N. sphaerocarpa* cover in 2016. Additionally, abundance of tenebrionid beetles in 2017 and species richness in 2018 exhibited positive correlations with *N. sphaerocarpa* cover (Table 4). Abundance of *B. gobiensis* was significantly and positively correlated with *N. sphaerocarpa* cover in 2016, 2017, and 2019. Additionally, abundance of *M. kraatzi alashanica* demonstrated a significantly positive correlation with *N. sphaerocarpa* cover, exhibiting variations with shrub species and sampling year (Table 4).

Table 3 Correlations of activity density, species richness, and tenebrionid beetles with mean precipitation and mean temperature at annual and monthly levels during 2015–2020

Index	Mean precipitation				Mean temperature			
	Annual		Monthly		Annual		Monthly	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Tenebrionid beetle community								
Activity density	0.66	0.156	0.31	**0.031**	–0.16	0.763	0.47	**<0.001**
Species richness	0.00	1.000	0.25	0.082	–0.15	0.781	0.43	**0.002**
Tenebrionid beetle species								
B. gobiensis	0.59	0.216	–0.49	**<0.001**	–0.09	0.872	0.46	**<0.001**
M. kraatzi alashanica	0.39	0.445	0.28	0.054	0.01	0.992	0.54	**<0.001**

Note: Significant differences of correlations are shown in bold.

4 Discussion

4.1 Rhythmic changes of tenebrionid beetles

Arthropods, including tenebrionid beetles, are the main invertebrate groups in desert ecosystems. They serve as key decomposers and provide essential food and water resources for vertebrates, thus contributing to the health and stability of desert ecosystems (Vonshak et al., 2009; Valdez, 2020; Sagi and Hawlena, 2021). Numerous studies have confirmed that tenebrionid beetles are the dominant arthropod group in arid and semi-arid desert areas globally, although significant regional differences exist in their composition and community structure (Polis, 1991; Whitford, 1993; Ragionieri et al., 2023). In the central part of the Hexi Corridor, 75.00% of tenebrionid beetle species are endemic to the Palaearctic region. Tenebrionid beetle community in the Gobi

Table 4 Correlations of activity density, species richness, and tenebrionid beetles with covers of *Reaumuria soongarica* (Pall.) Maxim. and *Nitraria sphaerocarpa* Maxim. during 2015–2020

Index	*R. soongarica*		*N. sphaerocarpa*	
	r	*P*	*r*	*P*
2015				
Tenebrionid beetle community				
Activity density	–0.09	0.465	0.17	0.146
Species richness	0.02	0.844	0.17	0.156
Tenebrionid beetle species				
B. gobiensis	–0.16	0.191	0.01	0.998
M. kraatzi alashanica	0.08	0.525	0.25	**0.033**
2016				
Tenebrionid beetle community				
Activity density	0.12	0.300	0.33	**0.005**
Species richness	0.23	0.052	0.25	**0.037**
Tenebrionid beetle species				
B. gobiensis	0.14	0.232	0.27	**0.024**
M. kraatzi alashanica	0.05	0.678	0.20	0.091
2017				
Tenebrionid beetle community				
Activity density	0.13	0.284	0.30	**0.009**
Species richness	–0.08	0.494	0.12	0.315
Tenebrionid beetle species				
B. gobiensis	0.14	0.250	0.31	0.008
M. kraatzi alashanica	0.08	0.482	0.14	0.256
2018				
Tenebrionid beetle community				
Activity density	0.31	**0.007**	0.05	0.689
Species richness	0.34	**0.004**	0.28	**0.016**
Tenebrionid beetle species				
B. gobiensis	0.12	0.299	0.01	0.960
M. kraatzi alashanica	0.13	0.289	–0.04	0.763
2019				
Tenebrionid beetle community				
Activity density	–0.22	0.065	0.10	0.386
Species richness	–0.15	0.206	0.06	0.605
Tenebrionid beetle species				
B. gobiensis	0.08	0.482	0.35	**0.002**
M. kraatzi alashanica	–0.24	**0.041**	–0.12	0.321
2020				
Tenebrionid beetle community				
Activity density	–0.12	0.313	0.14	0.256
Species richness	–0.15	0.217	0.02	0.859
Tenebrionid beetle species				
B. gobiensis	0.07	0.563	0.15	0.217
M. kraatzi alashanica	–0.06	0.599	0.01	0.940

Note: Significant differences of correlations are shown in bold.

desert is primarily composed of *B. gobiensis*, *A. sternalis*, *P. loczyi*, and *M. kraatzi alashanica*. This composition slightly differs from that of tenebrionid beetle communities in adjacent desert habitats (Liu et al., 2015), but resembles the findings from Yanchi, Ningxia Hui Autonomous Region (Yang et al., 2012). Tenebrionid beetles are a key beetle group in desert ecosystems, as demonstrated in areas like Ningxia Hui, Xinjiang Uygur autonomous regions, and other deserts (Polis, 1991; Lou et al., 2011; Yang et al., 2012). However, notable differences exist in species composition and abundance changes (Cloudsley-Thompson, 2021). In the central Hexi Corridor, tenebrionid beetles accounted for 19.50% of the total number and 77.00% of the biomass of arthropods (Liu et al., 2010). Lin et al. (2022) found that birds in the Gobi desert were mainly active during plant growing season, and that their monthly relative multiplicity index was closely related to the number of tenebrionid beetles. Beetle remnants have been found in bird and mammalian faeces, highlighting their role in the food web structure and functional dynamics of desert ecosystems. Although the number of tenebrionid beetle species in the Gobi desert showed little annual variation, the capture rates fluctuate significantly, which can be attributed to the reproductive changes of the main species driven by changes in precipitation and temperature. We also found that *P. victori* was only captured in 2020 in the Gobi desert, suggesting that changes in precipitation may affect the activity of rare tenebrionid species. In summary, although the species composition of tenebrionid beetles in the Gobi desert exhibited little annual variation, significant seasonal variations in capture quantity and monthly activity patterns among different species affected the community dynamics.

Interspecific differences in daily activity rhythms among the main beetle species in the Gobi desert are associated with their distinct survival strategies for coping with high temperature and drought stress (Parker and Lawrence, 2001). Tenebrionid beetle species have long adapted to extreme desert environments, and their unique physiological and ecological characteristics result in variations in activity rhythms, influencing dynamic changes in the tenebrionid beetle community (Ren et al., 2024a). Most tenebrionid species are nocturnal, and in this study, we found that *B. gobiensis*, *C. chinensis*, and *M. kraatzi alashanica* are mainly active at night, but *B. gobiensis* and *C. chinensis* are also active during the daytime on rainy days, suggesting that daily variations in temperature determine the daily activity rhythms of tenebrionid beetles (Cloudsley-Thompson, 2021). Medium-sized tenebrionid beetles like *A. sternalis* and *P. loczyi* are primarily active during the daytime in spring and summer. During periods of intense midday heat, they use shrubs or animal nests to avoid the temperature stress; this is related to their sheath wing structure and physiology structure, which can adapt to high temperature (Cloudsley-Thompson, 2021). Their coleopteran structure and metabolic activities allow them to withstand temperature and solar radiation stress during the daytime. Day-active beetle species in deserts also use microhabitats such as shrubs and vertebrate nests to avoid high temperature at midday. Some beetle species burrow into the ground to avoid heat stress. Beetle species active at dawn not only avoid heat stress but also use their coleopteran features to condense water vapour from the air to resist drought stress (Zotov, 2017). *B. gobiensis* and *M. kraatzi alashanica* are mainly active at night, and cloudy and rainy days, indicating that daily temperature changes govern their daily activity rhythms. Moreover, environmental changes can affect the daily activity rhythms of tenebrionid beetle species (Krasnov and Ayal, 1995). In summary, daily temperature changes are the primary factor influencing the activity rhythms of tenebrionid beetles, with their physiological and ecological traits driving their adaptive strategies. Monthly activity period of beetles in the Gobi desert spans from March to October, with some annual variations. Changes in temperature during spring and autumn likely serve as the main environmental factors limiting adult beetle activity. Activity period of beetles in the central Hexi Corridor can last up to 8 months. Dominant beetle species, such as *B. gobiensis*, *A. sternalis*, and *M. kraatzi alashanica*, exhibit longer activity periods than other species, consistent with findings from the Negev Highlands in Israel (Aldryhim et al., 1992). Sackmann and Flores (2009) observed significant monthly variations in the capture numbers of tenebrionid beetles in the shrubland and grassland of Patagonia, Argentina, although the species richness was less varied, which slightly differed from the findings of this

study (Sackmann and Flores, 2009). Our findings indicated that although the activity period of tenebrionid beetles exhibited little annual variation, there were significant annual and monthly changes in the number of tenebrionid beetle and species richness, which can be attributed to the different monthly and annual activity patterns of different species. Peaks in the number of different tenebrionid beetle species in the Gobi desert occur in spring and summer, with notable annual variations. This result differed from that observed in the deserts of Saudi Arabia and Argentina (Thomas, 1979), but aligned with seasonal variations of armoured beetles in the desert of central USA, Israel, and coastal sand dunes in Italy (Mazía et al., 2006). Additionally, a study on Simpson Desert in Australia found significant seasonal variation in energy density of beetles, with higher values in autumn than in spring (Gibb et al., 2019). *M. kraatzi alashanica* and *B. gobiensis* are two main species of tenebrionid beetles in the Gobi desert. These species differ in size and exhibit unimodal or multimodal monthly activity periods. In this study, the peak period of monthly activity was found in both spring and summer during 2015–2020. *B. gobiensis* is large in size with a 2–3-a life cycle; *M. kraatzi alashanica* is characterized by a 1–3-a life cycle, and changes in precipitation and temperature can affect the reproduction of these species, which in turn affects the annual and monthly changes in their population size (Fallaci et al., 2002; De Los Santos et al., 2006). Percentages of *B. gobiensis* and *M. kraatzi alashanica* accounted for 65.20%–88.30% of the total tenebrionid beetles, and their abundance significantly influenced the monthly and annual dynamics of tenebrionid beetle community. The short-term and long-term enrichment changes of litter resources driven by precipitation have important impacts on the growth and overwintering of beetle larvae in tenebrionid beetles, which may in turn affect the community dynamics of these beetles (Henschel, 2021). In addition, long life cycle species of tenebrionid beetles also exhibit lagged response to annual precipitation changes, thereby affecting the long-term response pattern of beetle community to precipitation changes (Maeno et al., 2014).

4.2 Spatial patterns of tenebrionid beetles

Vegetation coverage in the Gobi desert is relatively low. The enrichment of food resources in micro-habitats such as shrubs and ant nests strongly influence the spatial distribution patterns of tenebrionid beetles. Previous studies have shown that shrubs and ant nests in the Gobi desert positively impact the activity of arthropods, including tenebrionid beetles, though this effect varies seasonally and depends on micro-environments (Liu et al., 2012; Feng et al., 2022). Most tenebrionid beetle species are active in spring and summer, when rainfall is low, and the presence of shrubs and interspecific differences can affect their distribution, which is consistent with the findings of Mazía et al. (2006). Desert shrubs reduce daytime temperatures and increase nighttime temperatures, providing suitable niches for beetle activity (Ingimarsdóttir et al., 2012). Large-scale hydrothermal conditions are regarded as a key factor in shaping the geographic distribution patterns of zonal vegetation and animal diversity (Yang et al., 2019). This study demonstrates that variations in precipitation and temperature influence the degree of shrub dependence among tenebrionid beetles, thereby altering their spatial distribution patterns, which is consistent with the result of Liu et al. (2012). Tenebrionid beetles are typical omnivorous insects. Precipitation and temperature-driven changes in shrub and ant nest micro-environments influence their spatial distribution patterns. Furthermore, the interactions among precipitation, temperature, and shrubs determine the distribution patterns of tenebrionid beetles across various spatial and temporal scales (Liu et al., 2012, 2015; Bartholomew and El Moghrabi, 2018). Soil in the Gobi desert is relatively hard, and microhabitats shaped by sand dunes near *N. sphaerocarpa* form important habitats for both adult and larval tenebrionid beetles. Leaves and litter of *R. soongarica* and *N. sphaerocarpa* also serve as critical food and water sources for tenebrionid beetles. Our results suggested that the monthly and annual variations in precipitation and temperature could affect the dependence of tenebrionid beetles on shrubs, thereby altering their spatial distribution pattern (Liu et al., 2012). The spatial distribution patterns of tenebrionid beetle community in the Gobi desert during 2015–2020 were primarily regulated by structural factors. Climatic factors, such as precipitation and temperature, exhibited a consistent response pattern.

Moreover, environmental heterogeneity could enhance species diversity and spatial aggregation of beetles. Influence of climatic factors on the small-scale spatial distribution patterns of surface beetles in the Gobi desert should not be overlooked (Yang et al., 2019). Furthermore, studies conducted at various spatial and temporal scales are essential for elucidating the structural characteristics of surface beetles in the Gobi desert (Zajicek et al., 2021). Gao et al. (2023) found spatial heterogeneity in carrion beetle communities regulated by both deterministic and nondeterministic processes, which is not consistent with this study. Spatial variability of ground beetles in the Gobi desert is entirely regulated by deterministic processes, likely due to extreme climatic environment. In years with lower annual precipitation, variable range distances are significantly greater for both tenebrionid beetle community and interspecific interactions. This result may be attributed to the changes in food resources and predation intensity, as fluctuations in precipitation and temperature can lead to food resource scarcity, prompting tenebrionid beetles to expand their variable range distances.

4.3 Factors influencing the distribution of tenebrionid beetles

Changes in precipitation and temperature have both short-term and long-term effects on the tenebrionid beetle community. These factors alter the dependence of tenebrionid beetles on shrubs, thereby affecting their spatial aggregation patterns (Ilsøe et al., 2017; Lin et al., 2022). Water is a crucial limiting factor for the distribution of animals in arid and semi-arid areas. Short- and long-term fluctuations in precipitation strongly affect the diversity of large invertebrates, such as beetles and ants. Different invertebrate groups respond differently to precipitation, with significant regional differences (Gibb et al., 2019; Yang et al., 2019; Feng et al., 2022). The unique climatic conditions in the Gobi desert influence the diversity of tenebrionid beetles in their habitats. Our research showed that increased precipitation significantly enhanced the activity density of tenebrionid beetles. The activity density of tenebrionid beetles peaked in 2019 and 2020, with species richness being higher in 2020 than in other years. Moreover, the activity density of tenebrionid beetles significantly increased during rainy season. The composition of ground beetle communities exhibited significant seasonal fluctuations, with notable changes in the abundance of major species. Years with increased precipitation can not only increase the number of captures of certain major ground beetle species but also enhance the species diversity of rare ground beetle species. In addition to the influence of precipitation on the tenebrionid beetle community, we found that temperature significantly affected the activity rhythms of these beetles. As some beetles tend to be thermophilic in desert environments, areas with higher mean temperatures typically exhibit higher species diversity (Lescano et al., 2017; Ren et al., 2024b). Adult beetles are particularly sensitive to small-scale soil temperature fluctuations, and low temperatures in spring and winter may limit their survival conditions (Zotov, 2017). Additionally, persistent high temperatures led to low soil moisture, while high water demand during the development of tenebrionid beetle larvae meant that soil moisture could not satisfy their developmental needs. This finding aligns with the results of the study by Wang et al. (2020) on the effects of environmental factors on the diversity of ground beetles in the vertical vegetation zones of the Helan Mountains, China. The reproduction of tenebrionid beetles can be maximized under optimal temperature and soil moisture conditions, while both low and high temperatures can diminish their activity frequency (Wang et al., 2020; Cloudsley-Thompson, 2021). Given that the larvae of tenebrionid beetles require a significant amount of water during their development, insufficient soil moisture may hinder their development. Consequently, the reproduction of tenebrionid beetles can be maximally promoted at appropriate temperatures. Our results indicate that the activity density and species richness of adult tenebrionid beetles are significantly and positively correlated with monthly mean temperature. The activity and diversity of *B. gobiensis*, *C. chinensis*, and *M. kraatzi alashanica* are significantly and positively correlated with the monthly mean precipitation and temperature, highlighting the notable influence of these factors on tenebrionid beetles. Shrubs was also an important factor in the spatial distribution of tenebrionid beetles, with large shrubs such as *N. sphaerocarpa* having a greater influence on

beetles' aggregation than *R. soongarica* (Liu et al., 2012). Shrub presence affects the aggregation of tenebrionid beetles by a variety of factors such as resource-driven, predation intensity-regulated, and temperature-stressed factors, whereas season, soil texture, and landscape structure have no significant effects (Mazía et al., 2006; Shelef and Groner, 2011; Bartholomew and El Moghrabi, 2018). The study also found that effects of precipitation and temperature on the aggregation of tenebrionid beetles was non-linear. In summary, changes in precipitation and temperature have both short- and long-term effects on the tenebrionid beetle community, influencing the spatial distribution patterns of tenebrionid beetles by altering their dependence on shrubs.

5 Conclusions

A total of 11,941 individual tenebrionid beetles from 8 species were captured in the Gobi desert, Northwest China during 2015–2020. The dominant species, i.e., the large-sized *B. gobiensis* and small-sized *M. kraatzi alashanica*, accounted for 65.30%–88.20% of the total catch. The active period of tenebrionid beetles spanned from March to October, with significant seasonal variations and interspecific differences in activity periods. Their spatial differentiation was primarily influenced by structural factors, such as temperature and precipitation. Dynamics of tenebrionid beetle community were related to annual and monthly variations in precipitation and temperature. Moreover, monthly capture number and species richness were positively correlated with the monthly rainfall and mean temperature. Moran's *I* value indicated that the tenebrionid beetle community in the Gobi desert exhibited spatial autocorrelation at a scale of 24.00 m. Spatial distribution of tenebrionid beetles was related with the coverage of *R. soongarica* and *N. sphaerocarpa*. In summary, variations in precipitation and temperature drive the activity rhythms of desert tenebrionid beetles. The interactions among precipitaton, temperature, and shrubs also affect the aggregation of desert tenebrionid beetles at different temporal and spatial scales.

Conflict of interest

ZHAO Wenzhi is an editorial board member of Journal of Arid Land and was not involved in the editorial review or the decision to publish this article. All authors declare that there are no competing interests.

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Appendix

Table S1 Number of individuals and relative abundance of tenebrionid beetles during 2015–2020 in the Gobi desert, Northwest China

Tenebrionid beetles	2015		2016		2017		2018		2019		2020	
	NI	RD (%)	NI	RD (%)	NI	RD (%)	NI	RD (%)	NI	RD (%)	NI	RD (%)
Anatolica potanini	12	0.80	14	0.80	18	0.80	9	0.70	18	0.70	11	0.40
Anatolica sternalis	328	21.80	138	8.20	178	7.80	76	6.00	138	5.30	250	9.70
Blaps gobiensis	804	53.40	608	36.10	1434	62.70	408	32.10	703	27.00	609	23.50
Cyphogenia chinensis	24	1.60	38	2.30	28	1.20	17	1.30	13	0.50	73	2.80
Microdera kraatzi alashanica	252	16.70	492	29.20	570	24.90	639	50.20	1592	61.20	1198	46.30
Platyope victori	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	2	0.10
Pterocoma loczyi	78	5.20	278	16.50	32	1.40	74	5.80	97	3.70	316	12.20
Sternotrigon kraatzi	8	0.50	118	7.00	28	1.20	50	3.90	39	1.50	129	5.00
Total individuals	1506		1686		2288		1273		2600		2588	
Total species	7		7		7		7		7		8	

Note: NI, number of individuals; RD, relative abundance.

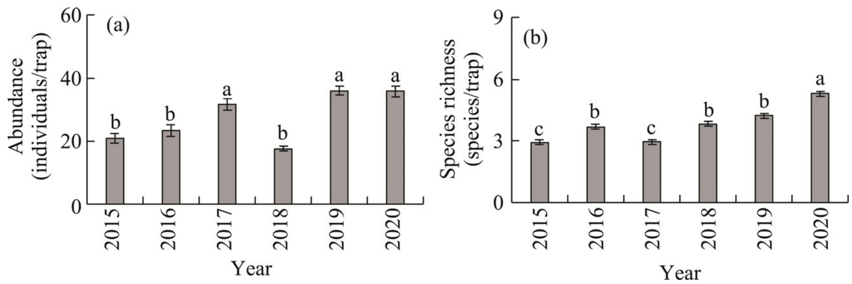

Fig. S1 Comparison of abundance (a) and species richness (b) of tenebrionid beetles during 2015–2020 in the Gobi desert, Northwest China. Different lowercase letters within different years indicate significant differences at *P*<0.05 level. Bars are standard errors.

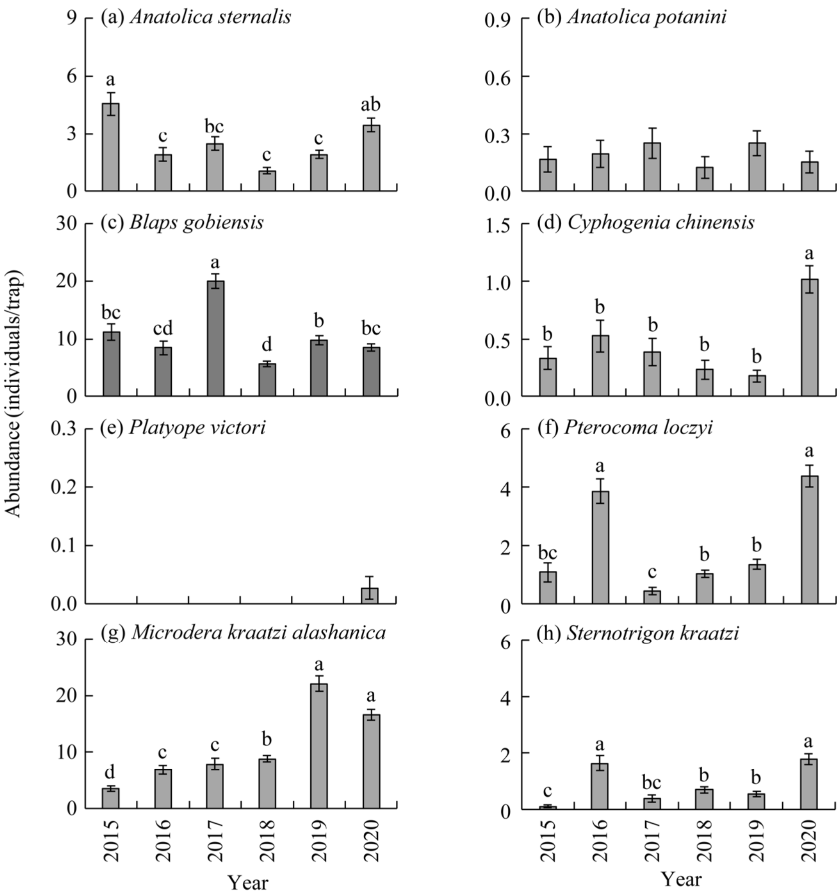

Fig. S2 Comparison of abundance of 8 species of tenebrionid beetles during 2015–2020 in the Gobi desert, Northwest China. (a), *Anatolica sternalis*; (b), *Anatolica potanini*; (c), *Blaps gobiensis*; (d), *Cyphogenia chinensis*; (e), *Platyope victori*; (f), *Pterocoma loczyi*; (g), *Microdera kraatzi alashanica*; (h), *Sternotrigon kraatzi*. Different lowercase letters within different years indicate significant differences at $P<0.05$ level. Bars are standard errors.